33. The Brain of the Zeuglodontidæ (Cetacea). By Raymond A. Dart, M.Sc., M.B., Ch.M., Professor of Anatomy, University of the Witwatersrand, Johannesburg; with a Note on the Skulls from which the Endocranial Casts were taken. By C. W. Andrews, D.Sc., F.R.S., F.Z.S., British Museum of Natural History.

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(Text-figures 1–24.)

Table of Contents.

	Page
1. Introduction	615
2. Material	616
3. The two Endocranial Casts unaccompanied by Osseous Remains	618
a. Zeuglodon sensitivus, sp. nov. (M. 12123.)	
b. Zeuglodon elliotsmithii, sp. nov. (M. 12066.)	
4. The three Endocranial Casts forming a Phyletic Series	627
a. Prozeuglodon atrox Andrews. (M. 9265.)	
b. Zeuglodon intermedius, sp. nov. (M. 10173.)	
c. Zeuglodon osiris Dames. (M. 10228.)	
5. Table of Measurements of the Endocranial Casts	634
6. The Zoological Position of the Zeuglodontidæ	635
7. Comparison of Zeuglodont and Prosqualodont Brains	638
8. The Trigeminus and the Law of Infiltration in Cerebellar Evolution	643
9. Note on the Skulls from which the Endocranial Casts were taken, by C. W. Andrews, D.Sc., F.R.S.	648
10. Bibliography	652

1. Introduction.

"The *Cetacea* are connected with the marine Carnivores through the genus *Zeuglodon*, as Huxley has shown, and the points of resemblance are so marked that the affinity cannot be doubted" (O. C. Marsh, 1877).

It has been suggested, in the past, that these water-living forms, which preserve in their skeletal parts characteristics linking them with the ancestors of modern Carnivora, were the actual ancestors of the whales and the dolphins, *i. e.*, the Cetacea. The Zeuglodonts were therefore grouped together as the Archæoceti. This suggestion of a Carnivore (or Creodont) ancestry seems to have been universally admitted until Matthew and Gregory (1910) pointed out various characteristics which

seem to link the Zeuglodontidæ more closely with Insectivore antecedents. In the meantime, the intimacy of the relationship between Zeuglodontidæ and Cetacea has been reaffirmed by numerous observers, including amongst many others Abel (1905–1913) and Winge (1919, 1921).

Previous investigation of the group has naturally centred around the osteological remains, and has shown (Andrews, 1907) that they probably arose "on the northern shores of the Ethiopian land in the early part of the Eocene period," and that "by the end of the Middle Eocene the true Zeuglodonts had come into existence, and had spread rapidly over the earth, their remains being found in the upper part of the Eocene of America, England, and New Zealand."

Since the appearance of Professor G. Elliot Smith's important contribution to the study of the form of the endocranial cast (1903) no new feature of the cerebral anatomy of these forms has been recognised, so far as I have discovered, although Stromer (1908) has figured what is apparently a unique natural endocranial cast in a form which he styles *Zeuglodon osiris*.

Shortly after the publication of Professor Elliot Smith's article, Mr. H. J. L. Beadnell gave him an almost perfect natural endocranial cast of a Zeuglodont collected in the Egyptian Fayum at the locality known as the Gar-el-Gehannem. Professor Elliot Smith kindly placed it at my disposal some time ago. I was assisted in the "development" of this natural cast by Professor D. M. S. Watson, who carefully removed most of the adherent bone and matrix, giving the result which has been accurately reproduced by Miss Davison in text-figs. 1, 2, and 3. This specimen has since been given to the British Museum by Professor G. Elliot Smith and is distinguished by the collection number M. 12123. The majority of the remaining figures have been drawn by Mr. Poulton, artist to the Anatomical Institute of University College, London.

Owing to the courtesy of the British Museum officials, of Dr. A. Smith Woodward, and especially of Dr. C. W. Andrews, who has assisted me at every turn in this work, I have been able to draw upon the paleontological resources of that institution. The Zeuglodont material there has been examined and extremely satisfactory casts made of the brain-cases, through the skilful work of Mr. L. E. Parsons.

The conclusion of this research would have been impossible apart from the courtesies that have been extended to me not only by the above-mentioned persons, but also by Sir Arthur Keith and Mr. Burne of the Royal College of Surgeons. To one and all I tender my grateful thanks.

2. Material.

One of the most important results that has emerged from the research is the definiteness with which we can now determine

certain different Zeuglodont species. The species *Zeuglodon osiris* Dames, 1894, was originally known from its lower jaw and certain other skeletal remains. Stromer (1903) correctly identified the skull of this creature, having in his possession an almost complete head. In a later paper, however, Stromer (1908) has caused confusion by referring an entirely different Zeuglodont to the same species. It became necessary, therefore, to discover which form actually was *Zeuglodon osiris* and, working with this information, to arrange our series.

In this matter two lines of evidence have substantiated our findings. Elliot Smith (1903) described an imperfect endocranial cast (M. 8150) which was known to have come from a skull (M. 8150) determined as *Zeuglodon osiris* Dames by Dr. Andrews in Egypt at that time. Fortunately, casts both of the cranial cavity and of the skull itself were amongst the British Museum material. In addition there were two skulls in the Museum, both of which were termed *Zeuglodon osiris*. A more intimate survey of these two skulls (M. 10228 and M. 10173) has rendered necessary their separation into two different species. Further, by means of the matrix in which they are embedded, Dr. Andrews is able to recognise them as probably coming from two entirely different beds of the Middle Eocene epoch. The first (M. 10228) possesses the same characters as M. 8150, and is actually *Zeuglodon osiris* Dames (see text-fig. 14) from the Qasr-el-Sagha Series. These two skulls (M. 8150 and M. 10228) conform entirely to the description of that type given by Stromer (1903).

This primary orientation having been achieved, it became apparent that the second skull (M. 10173), hitherto classed indiscriminately as *Zeuglodon osiris*, was not *Zeuglodon osiris* but another form altogether. The matrix in which it is embedded shows that it probably comes from the Birket-el-Qurun Series (Operculina-Nummulite beds). Its characters are intermediate between those of *Zeuglodon osiris* of the Carolia beds and *Prozeuglodon atrox* Andrews (M. 9266) from the Ravine beds. The endocranial casts confirm these facts; indeed, it was the serial conformity of the casts which led us to a re-examination of the osteological features.

Therefore, three of the endocranial casts here described come from skulls whose osteological features are known. Further, as a group, these three skulls and their casts may be conveniently regarded as a phyletic series. In view of this fact, Dr. C. W. Andrews has kindly written an account of the osteological features of the new form (M. 10173), which we will call provisionally *Zeuglodon intermedius*, sp. nov., and has stated its geological horizon to have probably been the Birket-el-Qurun series (*vide* p. 35, 'The Topography and Geology of the Fayum Province of Egypt,' H. J. L. Beadnell, Survey Department, Cairo, Egypt, 1905).

3. The Two Endocranial Casts unaccompanied by Osseous Remains.

Unfortunately there are no bony remains associated with the natural cast (M. 12123) spoken of at the outset. This cast, although belonging to some Zeuglodont, is so entirely different from any one of the phyletic series that it certainly comes from a species of Zeuglodont not known in the British Museum collection. Lack of information prevents our associating it with any other Zeuglodont hitherto described. This cast presents characters which indicate its affinity with the natural cast (M. 12066) described by Elliot Smith (1903)—which also was unaccompanied by any osseous remains—rather than with any member of this so-called phyletic series. This natural cast does not come from another member of the same species as that described by Elliot Smith, nor is it an endocranial cast of *Zeuglodon osiris*. Comparison with a duplicate (M. 12066) of the natural cast described by Elliot Smith and with *Zeuglodon osiris* (M. 10228) demonstrates a wider degree of separation from both of these than could be accounted for on a specific differentiation alone; we may be dealing here with different genera.

In the case of these casts (M. 12123 and M. 12066) the absence of knowledge concerning the skeleton and the exact horizon from which they have come makes it an invidious matter to establish new species. At the same time it is necessary, in order to avoid confusion in description, to associate some name with each of these casts since they represent at least different species, if not genera. Since we owe to Professor Elliot Smith our first detailed account of the brain in the Archæoceti, and especially the recognition that "the differences" (*i. e.*, between the endocranial cast of *Zeuglodon osiris* and the natural cast (M. 12066) in his hands) "are sufficiently pronounced to indicate a generic distinction between the two specimens"; I propose to term the form from which this type of cast is derived *Zeuglodon elliotsmithii*, sp. nov. The second natural cast (M. 12123)—the one which Professor Elliot Smith has given to me for description—I will call *Zeuglodon sensitivus*, sp. nov., since it was in this cast that a marked hypertrophy of the trigeminal apparatus was first recognised.

3. *a*. Zeuglodon sensitivus, sp. nov. (M. 12123.)

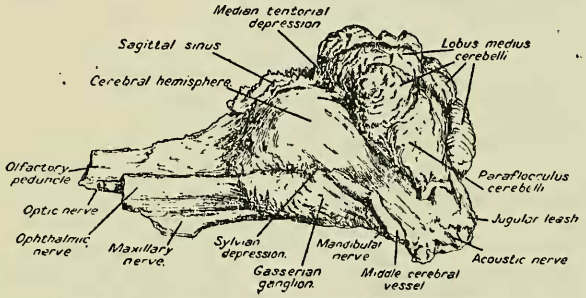
The most complete endocranial cast of a Zeuglodont yet discovered is that represented by Stromer (1908) *in situ* in the skull of what he has there called *Zeuglodon osiris*. It is not the *Zeuglodon osiris* of his earlier (1903) paper, but more nearly resembles the *Prozeuglodon atrox* Andrews or is intermediate between *Prozeuglodon atrox* and the *Zeuglodon intermedius* of this paper.

The peculiar resemblance of the general configuration of the fore-brain and olfactory peduncles in the Zeuglodont brain to

the corresponding regions of the reptilian brain was emphasized by Elliot Smith (1903), and is shown to distinct advantage in the lateral aspect of the natural endocranial cast (text-fig. 1) here under description.

This appearance is accentuated by the apparently reptilian "lobus olfactorius" formed by the anterior part of the cerebrum in Stromer's specimen. This particular resemblance is probably superficial. Instead of passing with a gradual expansion into the front end of the hemisphere as the stalk of a pear is attached to the smaller end of the fruit, the olfactory peduncle in the Zeuglodont is attached to the hemisphere on its ventral surface in the characteristically mammalian fashion, in front of the area of which the still prominent tubercula olfactoria form a part (see text-fig. 3). Behind the position of the attachment of the olfactory peduncle there is an obvious depression in the lower and anterior part of the lateral aspect of the cerebral hemispheres, which I consider to be a definite Sylvian depression (in the sense

Text-figure 1.



Lateral view of natural endocranial cast of *Zeuglodon sensitivus*, sp. nov. M. 12123. About ⅓ nat. size.

that that term is used in the lower Mammalia). This view is corroborated by the fact that the groove is occupied by the large middle cerebral vessels. Stromer's specimen shows not merely a large portion of the endocranial cast, but also a mould of the whole interior of the brain-case, including the olfactory peduncle from its origin in the olfactory bulb in its insertion into the brain. The length of the olfactory peduncle there is more than double the antero-posterior length of the cerebral hemispheres themselves, while the relative size and shape of the bulbar terminal dilatation is clearly distinguishable.

I am able to recognise in this cast (M. 12123) that the optic nerves formed the basal angles of Elliot Smith's "prismatic olfactory peduncle" (*vide* "anterior view" inset to text-fig. 2). Although this involves a considerable reduction of the actual dimensions of the olfactory peduncles in cross-section, as stated by Elliot Smith, it is still obvious that the sense of smell was of significant importance to the Archæoceti.

"Zeuglodon ist mindestens zu den hemianosmatischen Säugethieren zu rechnen im Gegensatze zu den anosmatischen Zahn- und Bartenwalen und ist auch durch normal verlaufenden Nasenrachengänge von letzteren unterschieden," says Stromer. In his insistence on the retention of a sense of smell by these creatures, he is justified even though his term "hemianosmatic" seems philologically meaningless.

Along the dorsal border of the lateral aspect of the cast the olfactory peduncle appears to merge into the sagittal sinus, which is continued over the cerebrum towards the anterior border of the cerebellum, where it dips into the "median tentorial depression" and receives veins from the cerebellar surface.

The cerebrum on either side is seen to be bounded by the sagittal sinus above and by the cerebellum posteriorly (which excludes all view of the mid-brain region from the dorsal or lateral aspect). Ventrally there is to be seen anterior to the region of the cerebellum designated "paraflocculus," a rounded roll-like structure continuous anteriorly with the ophthalmic and maxillary divisions of the trigeminal nerve. This bulging mass is a huge *Gasserian ganglion* which rivals the cerebral hemisphere in size, helps to mould the lateral contour of the brain-case, and gives rise to its three proportionately large trunks. Coursing over the lateral aspect of the Gasserian ganglion (well illustrated in text-fig. 1) are the middle cerebral vessels. Between these confines (sagittal sinus above, cerebellum behind, and Gasserian ganglion below) in *Zeuglodon sensitivus* the cerebrum bulges out, displaying a perfectly smooth hemispherical surface with the exception of the previously noted Sylvian depression.

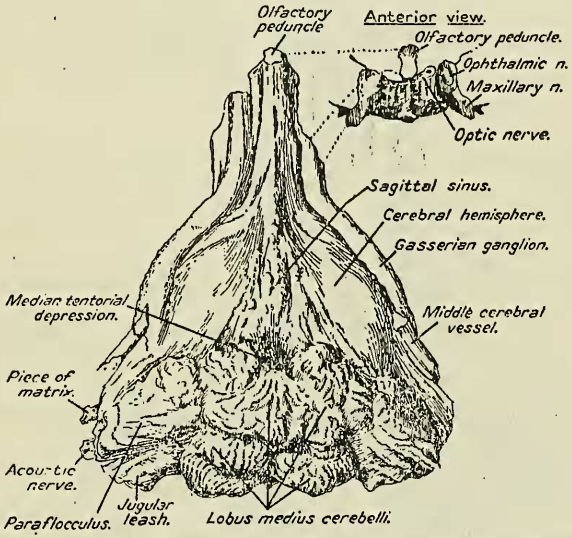
Behind the cerebrum lies the apparently irregular mass of the cerebellum elevated to a height of approximately 15 mm. above the cerebrum. From this it is separated by a tentorial sulcus, which is of especial depth in the mid-line, forming a "median tentorial depression." The most obtrusive feature of the cerebellum from the lateral aspect is unquestionably the lobus flocculares (consisting of the flocculus and the paraflocculus).

Elliot Smith has called this region the "paraflocculus" in his description of the Zeuglodont brain, and this name is retained in these figures. It seems that in most aquatic mammals the paraflocculus is the portion of the lobus floccularis which undergoes greatest expansion. The term paraflocculus may therefore be regarded, for the purposes of this paper, as synonymous with the lobus floccularis.

Despite Bolk's association of the paraflocculus with tail-movements, bears which have no tail (as Elliot Smith has pointed out to me) have, nevertheless, a well-marked paraflocculus. But, whereas the paraflocculus is present in most land-mammals, it becomes especially hypertrophied in all marine Mammalia irrespective of the stock from which they have sprung. Thus creatures so divergent as *Otaria* and *Monachus* (Carnivore), *Trichechus manatus* (of Ungulate origin), and *Phocæna* (probably

of Insectivore origin) all possess hypertrophied paraflocculi. This convergent hypertrophy of the same cerebellar region must arise from some cause common to all. Ferrier was one of the first to emphasise the functions of the cerebellum as primarily concerned with equilibration. Ingvar (1918) has supported this conception, and he finds a certain pattern of equilibratory localisation in the organ. This pattern is that of a "compass," a lesion in any given part of the cerebellum entailing a defect in co-ordinating muscle-movement in such a way as to resist falling in that direction; *i. e.*, the animal falls in the direction indicated by the site of the lesion. This theory seems adequate to account for the paraflocculus expansion exhibited by marine Mammalia, for

Text-figure 2.



Dorsal and anterior views of natural endocranial cast of *Zeuglodon sensitivus*, sp. nov. M. 12123. About ⅓ nat. size.

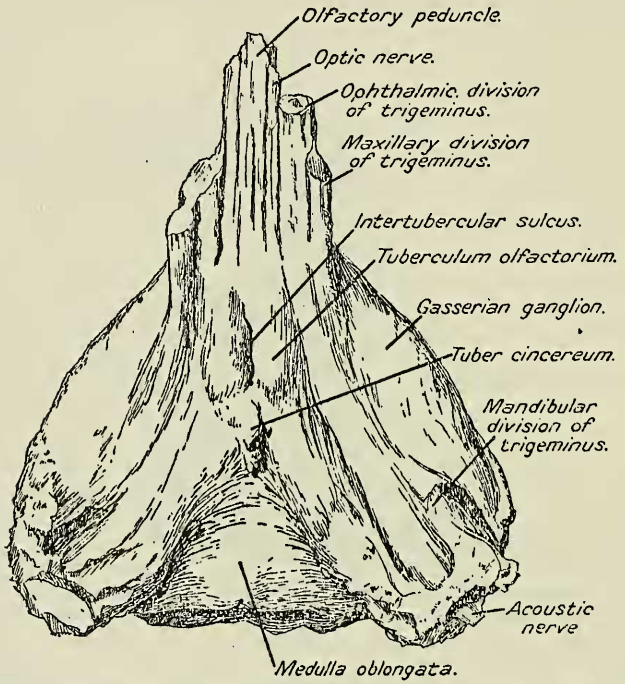
the paraflocculus is situated entirely laterally in the cerebellum, and these creatures are under the necessity of resisting continuously the tendency to "rolling," which the fluid medium postulates. In brief, it is a mechanism evolved to preserve *an even keel.*

The "paraflocculus" is bounded above by the region which in the subsequent account is referred to as the lobus medius. Anteriorly, the paraflocculus abuts on the cerebrum and the Gasserian ganglion; inferiorly, upon the eighth nerve and the petrous temporal and the casts of the foramen lacerum medium and the foramen lacerum posterius ("jugular leash" of the figures). Posteriorly, it is in contact with the exoccipital bone.

Medially from this region can be seen an elevation of the lobus medius of the cerebellum, which is the most posterior structure from the lateral aspect. It probably corresponds to the region which gives rise to the cerebellar tonsil of human anatomy.

Text-fig. 2 presents all those features emphasized by Elliot Smith (1903) in his specimen (*Zeuglodon elliotsmithii* of this paper). This natural cast reproduces very faithfully the convolutional pattern of the cerebellum and the position of the various meningeal vessels, particularly the sagittal sinus. This latter

Text-figure 3.



Ventral view of natural endocranial cast of *Zeuglodon sensitivus*, sp. nov. M. 12123. About ½ nat. size.

structure was described by Elliot Smith (1903) as the "dorsal rostrum." The knob-like elevations along its course are apparently veins entering it from the diploe of the skull. They bear an extraordinary resemblance to human Pacchionian bodies. Posterior to the prominence of the sagittal sinus and separating it from the cerebellum is again seen the deep "tentorial median depression" already referred to, from which the tentorial sulcus runs laterally on each side separating cerebrum and cerebellum. From this aspect, too, the cerebellum is seen in complete detail—

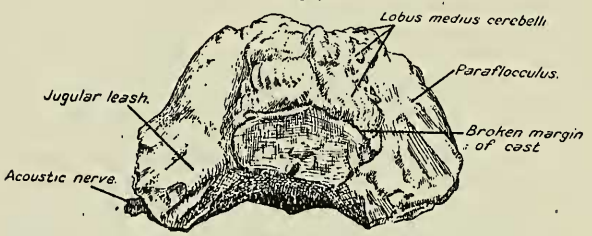
the enlarged lobus floccularis on either side and in the mid-region the so-called lobus medius. The lobus medius of the cerebellum is shown to be markedly asymmetrical. A bilaterally symmetrical projection into the posterior part of the tentorial median depression possibly represents the lobulus simplex of Bolk. If so, it is very small, and the lobus anticus is completely hidden from sight underneath it.

The hemming in laterally and anteriorly of the hemispheres at their ventral margins by the Gasserian ganglia is obvious from this aspect—forming a unique arrangement for a mammal. In no other mammal have these ganglia been described as visible from the dorsal aspect of the brain. The ganglia therefore are peculiar as constituting a factor in the modelling of the roof of the cranial cavity.

The ventral surface of the natural cast (text-fig. 3) gives important confirmation of the inferences drawn already. Through this cast we are able to infer the extent and size of the huge Gasserian ganglia. With these must be related a correspondingly extensive area of grey matter in the medulla oblongata and cord (substantia gelatinosa Rolandi). The resemblance of this aspect of the casts to the ventral surface of the brain of *Ornithorhynchus* (which is the only mammal that provides a suitable comparison, by virtue of its similar functional specialisation) is undoubtedly the clue in this arrangement. Anteriorly, the ophthalmic trunk of the trigeminus overlaps the optic nerves and olfactory peduncles. The course of all three structures is parallel for some distance until the region of the tuberculum olfactorium is reached. The maxillary division of the trigeminus is there attached to the ganglion? Between the ganglion and the tuberculum the optic nerve (not visible as a distinct elevation on the surface of the cast) must have skirted the lateral aspect of the tuberculum till it reached its posterior margin, where it bent medially to meet its fellow of the opposite side in the optic chiasma, the position of which can be recognised at the posterior end of an "inter-tubercular sulcus" lying in the mid-line between the two tubercula. Directly posterior to this point there is a single median elevation present in the three casts. It is obviously the site of the strongly-marked tuber cinereum and hypophysis. Behind this region the Gasserian ganglia diverge, giving place first of all to a slight central depression, then to a broad flat surface. This wide divergence and a bulging of the cast on either side of the mid-line may be due in large measure to the forward jutting of a tuberculum quinti upon either side correlated in size with the enormous Gasserian ganglia. In the cast we have no indication that an elevation due to a pons Varolii, as such, was present, and probably it possessed no larger pons than the Prototherian. The "bulging of the cast" postero-medial to the Gasserian ganglion may therefore be interpreted as the upper portion of the tuberculum quinti. Behind it lies a transversely running depression in the region where the pons would normally lie. It is possible that this

depression is due to the constricting influence of a small pons, such as was probably present. In other words, the substantia gelatinosa expanded anterior and posterior to this site to form the prominences evident in the cast. More posteriorly the base of the brain passes gradually into the medulla oblongata. In many mammals (*e. g.*, Ungulata) the transverse width of the medulla oblongata is very appreciable, but in these creatures the transverse width is never so great (relatively) as in animals (e. g., *Ornithorhynchus*) which rely to a greater extent upon the "fifth nerve sense." The great increase in transverse width found in the Zeuglodontidæ is to be regarded as a corroboration of the observation already made concerning the size of the tuberculum quinti. In the cast there is no trace of the origin of either the third, fourth, or sixth cranial nerves. The origin of the seventh and eighth is also obscure, though the latter is exposed for a portion of its course through the petrous portion of the temporal bone. The cast ends abruptly before the emergence of the IX, X, and XI complex of cranial nerves. The study of the skeletal parts

Text-figure 4.



Posterior view of natural endocranial cast of *Zeuglodon sensitivus*, sp. nov. M. 12123. About ⅓ nat size.

confirms what has been stated concerning the splaying apart of the Gasserian ganglia (and incidentally of the posterior parts of the cerebral hemispheres and the lobi flocculares of the cerebellum) by the expansion of the tubercula quinti.

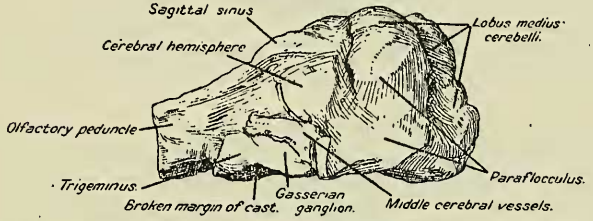
No new anatomical feature from this aspect (text-fig. 4) is revealed. The natural cast has been severed transversely at the hinder end of the cerebellum. The important fact to be remembered is that the lobus anticus and lobus posticus are probably totally hidden from external view; and the central mass of the cerebellum, as exhibited in dorsal or posterior view, is composed entirely of the lobus medius (of Elliot Smith), while laterally on either side lies the lobus floccularis. Posteriorly to the acoustic nerve and ventrally from the lobus floccularis ("paraflocculus" of the text-figures) is to be seen an ill-defined mass, which represents the cast of the jugular vein and the associated nerve-structures, which finally emerge at the foramen lacerum posterius. I have called this region the "jugular leash."

3. *b.* Zeuglodon elliotsmithii, sp. nov. (M. 12066.)

Turning now to the lateral view of *Zeuglodon elliotsmithii*, M. 12066 (text-fig. 5), and comparing it with *Zeuglodon sensitivus* (text-fig. 1) we recognise in both the general Zeuglodont characters, which may be summarised as including a hypertrophied cerebellum tending to grow forwards over the cerebrum, hypertrophied trigeminal apparatus, and a diminutive reptilian-like cerebrum bounded by the two former behind and below, and an unusually well-marked sagittal sinus above and in the mid-line.

It will be noted that in *Zeuglodon elliotsmithii* the fore brain is very flattened and slopes upwards and backwards evenly towards the cerebellum, that the cerebellum is only slightly elevated (1–10 mm.) above the flattened cerebrum, and that appears almost vertical from the lateral aspect. In all these features this brain contrasts strongly with that of *Zeuglodon sensitivus*. Further, the trigeminal apparatus, although hypertrophic,

Text-figure 5.



Lateral view of endocranial cast of *Zeuglodon elliotsmithi*, sp. nov. M. 12066. About ⅓ nat. size.

does not seem quite so pronounced as in *Zeuglodon sensitivus*, although the fragmented nature of the cast, in this region, renders a final statement upon this particular point impossible.

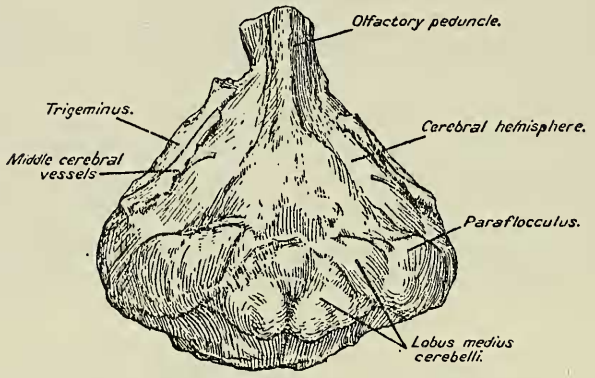
The features to which reference has been made are to be recognised from the dorsal aspect also. Note further from this aspect that the lobus medius cerebelli of *Zeuglodon elliotsmithii* is symmetrical, whereas the other is markedly asymmetrical (*cf.* text-fig. 2), a point which is also clearly evidenced in the posterior views (text-figs. 4 and 7).

As these figures have been drawn to scale it is clear that many features, such as the general flattening of *Zeuglodon elliotsmithii*, shown by the increased bi-paraflocculär width, its general triangular outline as seen from the dorsum, and its slender transversely-elongated cerebellum mark the brain as characteristic and distinct from that of *Zeuglodon sensitivus*. These facts are brought out by a comparison of the table of brain-measurements (*vide infra*). Thus both the greater width and length of the cerebral hemispheres emphasize the flatness already referred to, while both the

total length and height of the brain-mass were considerably smaller in this species.

The bulk of the endocranial cast (average of five separate measurements by water displacement) of *Zeuglodon elliotsmithii*

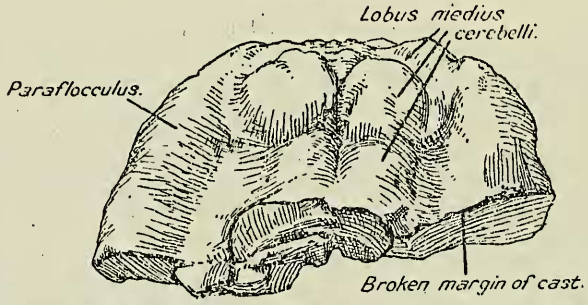
Text-figure 6.



Dorsal view of endocranial cast of *Zeuglodon elliotsmithii*. M. 12066. About ⅓ nat. size.

was 300 c.c. Elliot Smith gives (1903) 410 c.c. as the bulk of this "natural cast (including that of a considerable quantity of matrix attached to the base of the brain and some small fragments of bone)," but states that the actual weight of the brain

Text-figure 7.



Posterior view of endocranial cast of *Zeuglodon elliotsmithii*. M. 12066. About ⅓ nat. size.

was probably "nearer 300 grammes." In this latter estimate I am inclined to agree. But whereas the bulk of *Zeuglodon elliotsmithii* could not have been very much greater than 300 c.c., that of the natural cast of *Zeuglodon sensitivus* (in which the medulla

oblongata is absent) was 490 c.c., or nearly 200 c.c. larger. This is of some interest not only in demonstrating the specific (if not generic) difference between these two Zeuglodonts but also in showing that the brain-capacity of certain Zeuglodonts was considerably greater than that of some existing Cetacea—because the brain-weight of *Kogia* (Haswell) is only 455 grammes.

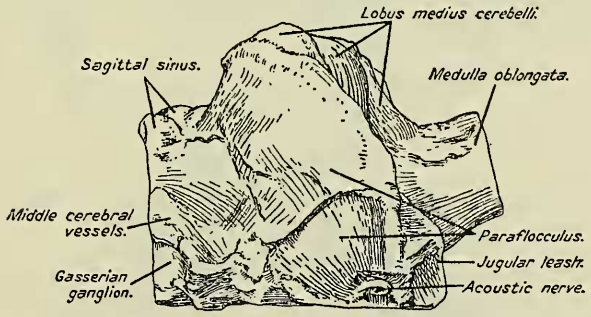
All these distinctions between these two forms are certainly not to be accounted for by a difference in the sex or age of the individuals. They should therefore be separated as distinct species, as has been done here, until fresh data shall be forthcoming when it may be possible to associate one or the other of these forms, *Zeuglodon sensitivus* or *Zeuglodon elliotsmithii*, with the species now recognised from skeletal parts alone, such as *Zeuglodon zitteli*.

4. The three Endocranial Casts forming a Phyletic Series.

4. *a*. Prozeuglodon atrox Andrews. (M. 9265.)

In the 'Descriptive Catalogue of the Tertiary Vertebrata of the Fayum of Egypt,' Dr. Andrews described briefly the outstanding features of this cast, pointing out its correspondence with Elliot Smith's general account of the Archæoceti (1903). It is unfortunate that in this important cast from the lowest bed

Text-figure 8.



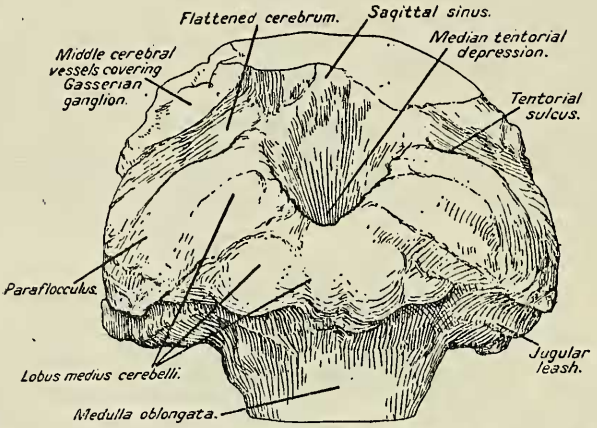
Lateral view of endocranial cast of *Prozeuglodon atrox* Andrews. M. 9265. About ⅓ nat. size.

of the Middle Eocene there is no reproduction of the anterior portion of the cranial cavity, because this region would supply important data concerning the degree of trigeminal specialisation in this early representative of the group—data which now must be inferred from the evidence afforded by other regions.

It is astonishing to find in this earliest-known Zeuglodont an extravagantly expanded cerebellum. It is the dominant portion of the brain from lateral, dorsal, or posterior aspects. It rises at

certain points taken along the tentorial sulcus to a height of 35 mm. above the cerebral surface and nowhere is it less than

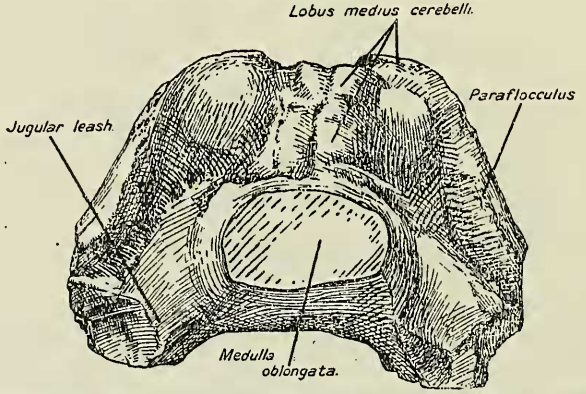
Text-figure 9.



Dorsal view of endocranial cast of 4. *a. Prozeuglodon atrox* Andrews. M. 9265. About ⅓ nat. size.

20 mm. higher than the cerebral surface. This one characteristic immediately brands this brain (however Zeuglodont in type) as something entirely distinct from what has hitherto been described

Text-figure 10.



Posterior view of endocranial cast of *Prozeuglodon atrox* Andrews. M. 9265. About ⅓ nat size.

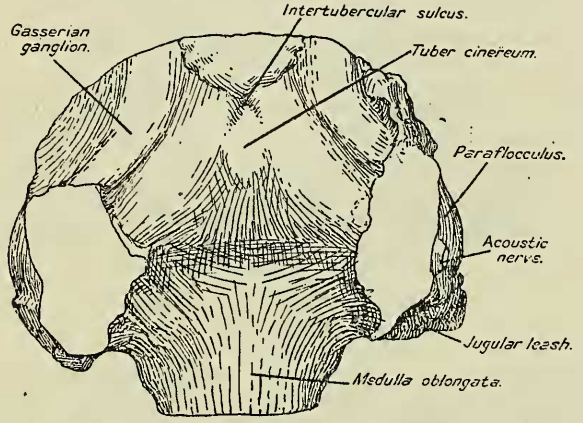
in the literature. The size of the cerebellum is immense and the size is not confined to one part of the organ only; the parafloc-

culus is hypertrophied, but so, too, is the lobus medius and, in addition, the latter is markedly asymmetrical.

These facts are readily appreciated from the figures. The lateral aspect is instructive as revealing the relative size of the cerebrum and the cerebellum. Coursing over the latter from the top to lateral angle is a ridge, probably indicating the site of a venous channel, which converges upon the jugular leash posterior to the acoustic nerve.

From the posterior aspect we are impressed with the vertical "lie" of the paraflocculi and their size relative to the lobus medius. The massive "jugular leash" undoubtedly accommodates the venous channels and the posterior cerebral nerves. The dimensions of the medulla oblongata should be noted for comparison with the later forms to be described.

Text-figure 11.



Ventral view of endocranial cast of *Prozeuglodon atrox* Andrews. M. 9265. About ⅓ nat. size.

The ventral view of *Prozeuglodon atrox* should be compared with text-fig. 3. It will then be recognised that the structures on the basal surface of *Prozeuglodon atrox* are entirely comparable with those found on the basal surface of *Zeuglodon sensitivus*. It is typically Zeuglodont in character—a fact which we will find to be of great significance in comparing these endocranial casts with that of Prosqualodon. No features call for special attention at this stage of the discussion other than those noted in the figures themselves.

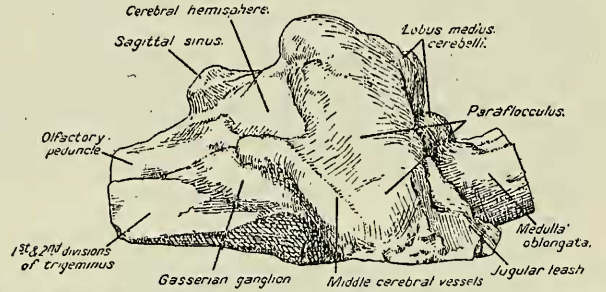
4. *b.* Zeuglodon intermedius, sp. nov. (M. 10173.)

Zeuglodon intermedius from the middle beds of the Middle Eocene shows from the lateral aspect features comparable in

most points with those of *Prozeuglodon atrox*, save for the more marked sagittal sinus, larger Gasserian ganglia, and a greater backward thrust of the paraflocculus.

From the dorsal aspect it is evident that there is a greater

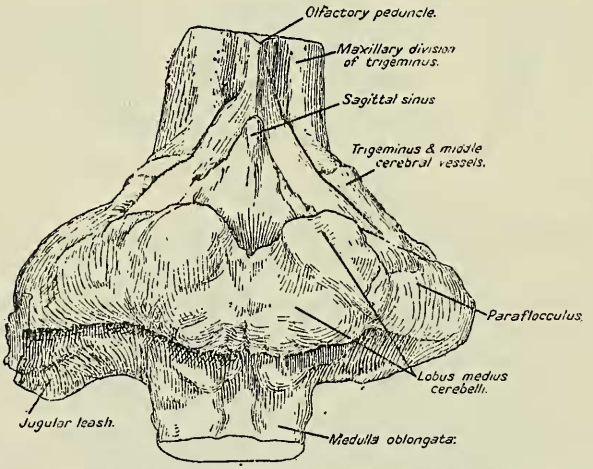
Text-figure 12.



Lateral view of endocranial cast of *Zeuglodon intermedius*, sp. nov. M. 10173. About ⅓ nat. size.

lateral thrust of the paraflocculi also, a fact still more emphasized in the posterior view. The prominence of the sagittal sinus is

Text-figure 13.



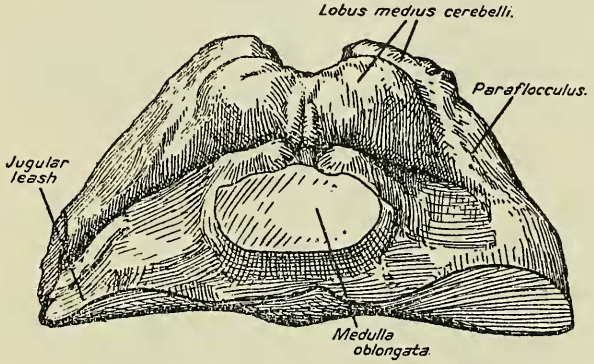
Dorsal view of endocranial cast of *Zeuglodon intermedius*, sp. nov. M. 10173. About ⅓ nat. size.

well shown from the dorsal aspect also, but the median tentorial depression is not quite so pronounced.

An arresting feature of this cast is the transversely running furrow subdividing the central mass of the cerebellum and

disappearing laterally below the paraflocculi. Here it separates the paraflocculus above from the structures of the jugular leash below. It is due to a kind of secondary tentorial bony projection on the interior aspect of the occipital bone. The presence of this bony strut is perhaps to be associated with the increasing width of the occipital region. This furrow is wider and more dorso-ventrally situated in the cast of *Prozeuglodon atrox*; whereas in *Zeuglodon osiris* (vide infra) it is still transverse but very wide and scalloped out, showing that with the extreme width of the skull of *Zeuglodon osiris* the bone has become greatly reinforced in thickness internally. It is well to note such cases as these

Text-figure 14.



Posterior view of endocranial cast of *Zeuglodon intermedius*, sp. nov. M. 10173. About ½ nat. size.

where the modelling of the skull undoubtedly influences the shape of the endocranial contents, because it shows that the interplay of factors (*i. e.*, brain upon skull and skull upon brain) in cavity-modelling is ceaseless and reciprocal.

Coincident with the lateral expansion of the brain-substance there has been no widening of the medulla oblongata or the aperture of the foramen magnum (*vide* Tables), but the thickness of the medulla oblongata has decreased somewhat and so it presents a somewhat more ellipsoidal transverse section.

The cubical capacities of these two casts was 790 c.c. for *Prozeuglodon atrox* and 785 c.c. for *Zeuglodon intermedius*. As the cast of *Prozeuglodon atrox* was very incomplete anteriorly it is evident that its cubic bulk must have been considerably over 800 c.c.

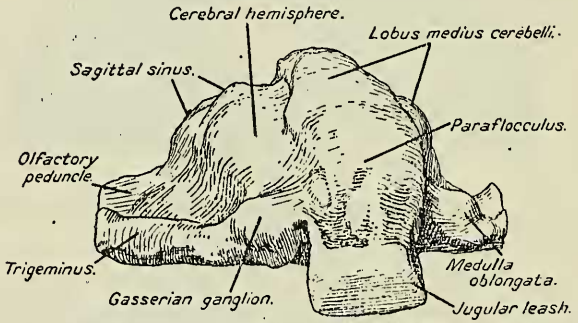
The degree of likeness between these two forms both cranially and endocranially is so great that they may be regarded as very closely related phyletically. Because of this the decreased volume of the brain of *Zeuglodon intermedius*, in accordance with the "law of increasing brain weight" expressed by Marsh, indicates

a degenerating condition in this later Zeuglodont type. When we realise that *pari passu* with this decrease in volume there is an actual increase in the lateral thrusting of the brain-mass and with it of the Gasserian ganglia, and a relative flattening of the mass of medulla oblongata, it seems clear that this degeneration is primarily trigeminal in nature.

4. *c.* Zeuglodon osiris Dames. (M. 10228.)

A comparison of the lateral aspect of the cast of *Zeuglodon osiris* from the upper beds of the Middle Eocene with the preceding forms is very striking. One gathers the impression that the brain-mass is shrivelled and shrunken, a conception that is strengthened by examination of the dorsal and posterior views. If we take the features seriatim we find first of all that the Gasserian ganglion is relatively small as compared with the other forms, but its stranded position (laterally to the cerebrum—see dorsal view) shows that this creature is descended from a type in

Text-figure 15.



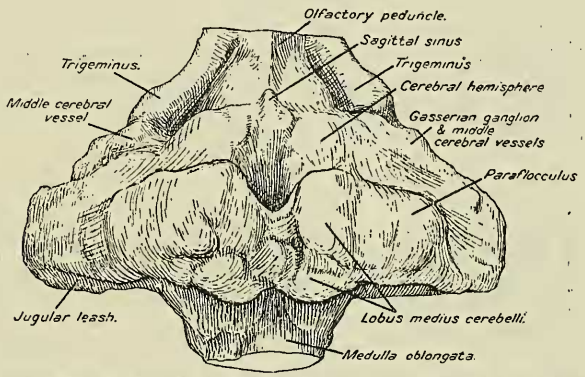
Lateral view of endocranial cast of *Zeuglodon osiris* Dames. M. 10228. About ⅓ nat. size.

which the trigeminal apparatus was of a much more imposing nature. The "gouged out" cerebrum reveals a degenerate condition of this organ. Obviously the olfactory region has become even more atrophied than in the other known Zeuglodonts. Despite the opportunity offered by this atrophy anteriorly and the diminished size of the cerebellum posteriorly the cerebrum is diminutive.

The cerebellum is still large but it is crumpled. The paraflocculi no longer bulge over the acoustic region, but are contracted towards the lobus medius. The latter is very asymmetrical. The space between the middle cerebral vessels and the jugular leash, and lateral to the paraflocculus, seems to have been devoid of brain-substance in the recent condition and to have been occupied by venous sinuses.

The lobus medius, or area crescens, is not only very asymmetrical but is poorly developed, and the paraflocculi form by far the greatest part of the cerebellar mass. The posterior view affords perhaps the completest picture of this atrophic brain, for here we recognise the general flattening out or "cake-like" appearance of

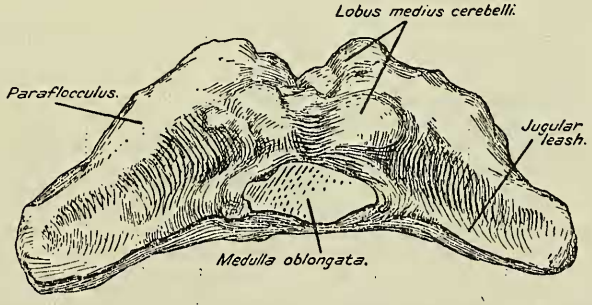
Text-figure 16.



Dorsal view of endocranial cast of *Zeuglodon osiris* Dames. M. 10228. About ⅓ nat. size.

this brain (which came from a perfect skull) and also the extremely long but narrow cross-section of the medulla oblongata. This view of the medulla oblongata coupled with the lateral view

Text-figure 17.



Posterior view of endocranial cast of *Zeuglodon osiris* Dames. M. 10228. About ⅓ nat. size.

of this region corroborate the inference we have already drawn that in *Zeuglodon osiris* we have the *degenerate offspring of a specialised race.*

The degree of this degeneration is perhaps most graphically shown if we compare the cubic capacity of this brain (480 c.c.)

5. Table of Measurements of the Endocranial Casts.

	M. 12123. *Z. sensitivus.*	M. 12066. *Z. elliotsmithi.*	M. 10228. *Z. osiris.*	M. 10173. *Z. intermedius.*	M. 9266. *Proz. atrox.*
Greatest width of cerebrum	87 mm.	92 mm.	94 mm. (approx.).	90 mm. (approx.).	95 mm. (approx.).
Greatest inter-parafloccular width	135 mm.	126 mm.	192 mm.	172 mm.	153 mm.
Length of cerebral hemisphere (measured to the tentorial sulcus)	56 mm.	64 mm.	52 mm.	47 mm.	42 mm. (approx.).
Height of cerebellar projection above the cerebrum along tentorial sulcus	10–20 mm.	1–10 mm.	15–20 mm.	20–25 mm.	20–35 mm.
Width of middle lobe of the cerebellum ... *a.* in the region of the Area B	91 mm.	100 mm.	60 mm. (approx.).	96 mm.	114 mm.
Width of middle lobe of the cerebellum ... *b.* in the region of the Area C	65 mm.	53 mm.	57 mm.	64 mm.	47 mm.
Width of medulla oblongata at foramen magnum	—	—	40 mm.	57 mm.	58 mm.
Height of medulla oblongata at foramen magnum	—	—	20 mm.	34 mm.	37 mm.
Greatest height of brain-mass from base to lobus medius cerebelli	73 mm.	66 mm.	65 mm.	96 mm.	96 mm.
Greatest antero-posterior diameter of cerebellum measured midway along tentorial sulcus	30 mm.	28 mm.	41 mm.	43 mm.	50 mm.
Greatest length of brain-mass	100 mm. (approx.).	97 mm. (approx.).	100 mm. (approx.).	108 mm.	110 mm. (approx.).
Cubic capacity	490 c.c.	310 c.c.	480 c.c.	785 c.c.	800+ c.c.

with those of the foregoing which are almost twice the size. An examination of the tables and the diagrams of the skulls will show that this discrepancy in brain-capacity is not due to any diminished bodily size in *Zeuglodon osiris*, for although the skull may be somewhat shorter it is absolutely wider than those of the other two forms.

One can only conclude that we have here an obvious dwindling in brain-substance which has affected not only the trigeminal and olfactory regions but with them the cerebrum, cerebellum, and the medulla oblongata. The whole evidence goes to show that the devolutional potentialities exhibited in the specialisations (chiefly trigeminal) of *Prozeuglodon* and the group it typifies have found in *Zeuglodon osiris* (M. 10228) their logical finale.

6. The Zoological Position of the Zeuglodontidæ.

Certain facts arising from our study of these endocranial casts claim our immediate attention. The first of these is the trigeminal specialisation. In all of the Zeuglodonts (although coming from different horizons) the essential features noted in *Zeuglodon sensitivus* apply. In all, the Gasserian ganglion assists in modelling the roof of the cranial cavity. The inference is justified that the group, as a whole, rested from the outset upon this specialisation for its subsequent achievements.

It seems to be a law of general evolutionary application that specialisation of one "sense" entails as its corollary the atrophy of one or more of the other avenues of sense-perception. Thus, birds become specialised as to sight but lose their appreciation of smell; the same is true, though in different ways, for Teleostean fishes and for Primates. In *Ornithorhynchus*, which specialises in its "fifth nerve sense," we find a relative atrophy of both smell and sight. In Zeuglodontidæ the sense of smell has certainly been largely lost as a result of their adoption of a water habitat, and it seems likely that sight also was of diminished value.

To the loss of smell and the abortion of the basal (olfactory) parts of the cerebrum with their effect in limiting the longitudinal extension of the hemispheres and consequently of the cranial cavity, reference was made by Elliot Smith (1902 and 1903). A relative loss of sight, with a resulting diminution of the mid-brain and thalamic regions, may assist in accounting for the smallness of the cerebrum in *Prozeuglodon* and also for its lack of growth in the two later forms from the upper horizons. It assists in the understanding of the propinquity of the cerebellum to—or, rather, its overgrowth over—the cerebrum, and affords further reason for the diminished longitudinal extension of the cerebral axis (because of a wasting mesencephalon and optic thalamus and the consequences entailed thereby) throughout the series.

But it seems to me that the lateral expansion not merely of the brain-stem itself but also of the cerebellum has been provoked mainly by the trigeminus, and that a specialisation of this nerve has been the most significant factor in determining the queer

contour of the Zeuglodont brain. Of course, the enlarged cerebellum has played a role in the lateral expansion of the cranial cavity, but the extraordinary dimensions, even for an Eocene animal, of this cerebellum can only be explained by the tribute coming from trigeminal nerves whose Gasserian ganglia rival the cerebral cortex in size. Hence the influence of the cerebellum is fundamentally trigeminal in origin.

It is true then that, although the trigeminus has played the chief part in this expansion, the internal factors include also an olfactory and a visual factor and may well have been assisted in Zeuglodonts, as Andrews (1908) suggested, by the "pressure on the anterior end, more or less in the direction of the long axis," during motion through the water, "and during very rapid movement this pressure must be considerable."

Now a reduction in value of the sense of smell and possibly of sight and a compensatory dependence upon the sense of touch in the muzzle—*i. e.*, a certain degree of trigeminal specialisation—are equally to be anticipated in the ancestors of modern Cetacea. Might it not be that the Zeuglodontidæ, in this respect as in their osteological conformity, are to be regarded as ancestral to Cetacea? This might be admitted if it were not for the demonstration of the already-marked specialisation of *Prozeuglodon atrox* and the gradual deterioration by specialisation within the phyletic series as already discussed. In this light the passage of Cetacean ancestors through a "trigeminal" stage in evolution can only be cited as convergence, or may be explained by the hypothesis that the Zeuglodontidæ and the true ancestors of Cetacea may have had a common ancestry in the earliest Eocene.

Despite the positive views concerning the ancestral relationship of Zeuglodontidæ to Cetacea stated at the outset, it must not be assumed that palæontologists are agreed concerning this interpretation.

As early as 1877 Marsh said: "That the connection (between *Zeuglodon* and Cetacea) was a direct one, however, is hardly probable, since the diminutive brain, large number of simple teeth, and reduced limbs in the whales all indicate them to be an old type which doubtless branched off from the more primitive stock leading to the Carnivores."

Weber (1886, p. 243) also referred to *Zeuglodon* as "einen verunglückten Versuch Cetaceen herauszubilden," and although there have been wavering opinions by many since, which even Weber himself has shared, many, such as Müller, Fraas, and Stromer, have enunciated the same view.

Fraas, in 1905, summed up the evidence to that date available and showed that the Zeuglodontidæ, arising from some possible Creodont stock, have passed through some stage corresponding to his *Eocetus* (*Mesocetus*) and, by differentiation, have produced various forms, including the gigantic ones which generally have marked the acme of evolutionary progress in many groups of animals, after which the race has disappeared. He has felt it

impossible to regard such later gigantic forms as ancestral to the later Squalodon series of animals, which appear to be more definitely related to the progenitors of the modern Cetacea. According to Winge (1919, 1921) Fraas "considered both *Protocetus* and with it other Zeuglodonts as a side branch from the Carnivores which did not lead in the direction of true whales."

Stromer (1908, p. 174) also states: "Ich halte also einstweilen für geboten die Zeuglodontidæ für eine ähnliche Parallelreihe der Denticeten anzusehen, wie sie neuerdings innerhalb vieler engeren Säugethier-abtheilungen nochgewiesen wurden. Sie hatten schon im Obereözan ihre Blütezeit unter Entwickelung von Riesenformen wahrend die anderen fast gleichartig aber viel weiter sich differenzierend langsamer sich entwickelten und wieder in mehrere Zweige auseinandergingen, die auch in vieler Beziehung einander parallel fortliefen. In diesem Sinne also nehme ich wie Weber (1886, S. 243) Zeuglodon als 'einen verunglückten Versuch Cetaceen herauszubilden' halte aber für noch nicht beweisen dass alle Archæoceti so auf zufassen wären."

Abel, in his later works (1913), does not appear to have any doubt that the Zeuglodontidæ lie off the direct line, with the possible exception of the so-called Microzeuglodontidæ. Because of their great specialisation, the degree of which would entirely unfit them for such an evolution, I am entirely in agreement with the opinion that no Zeuglodont here examined can be regarded as ancestral to Cetacea.

It is a curious fact that these highly specialised animals have so wide a geological distribution, and one in favour of their marine life. This wide distribution may have occurred before the trigeminal specialisation, so characteristic of all these Fayum forms, was attained. This makes the examination of the endocranial casts in Zeuglodontidæ found elsewhere in Europe, in America, and in Australia of the greatest importance because the facts put forward demonstrate our lack of knowledge concerning the evolutionary history of the whales and also because "the distribution of the Zeuglodontidæ and other shallow-water fauna" has been used (Stromer, 1906, and Andrews, 1907) to indicate the location of the shore-lines of previous land-connections between the Old and New Worlds. I consider that in the demonstration of this tactile specialisation in Zeuglodonts their restriction to a shore-line distribution is shown to be highly probable.

The parallel origin of the Zeuglodontidæ and the Sirenia—probably in the Lower Eocene—is very striking. The grade of cerebral organisation in both is approximately similar, but the cerebellum of Zeuglodontidæ seems to indicate that its life was somewhat less retired than that of Sirenia. Andrews (1907) has shown that "freedom from competition and, to some extent, from powerful enemies, would offer exceedingly favourable conditions for the rapid spread and multiplication" of these groups in the Eocene seas. Thus both groups became widely disseminated, but

whereas the Sirenia have persisted as "living fossils," despite their humble grade of intelligence, the Zeuglodontidæ have long since disappeared.

This disappearance is to be correlated with the fact that, whereas the Sirenia chose an eminently retired and sluggish mode of existence, the Zeuglodontidæ were more active. They came into more direct conflict with other marine forms and, specialised as they were, did so at a disadvantage and were overwhelmed in the struggle for existence.

The present study therefore indicates that the scepticism of Marsh and Fraas was entirely justified and that Winge (1921) is incorrect in regarding the Zeuglodontidæ as ancestral to Cetacea. The origin, dispersal (into so many strikingly different forms and all over the globe), and disappearance of this group geologically is a demonstration of the conception put forward by Marsh (1877) that "In every primitive type which was destined to survive many geological changes there seems to have been a tendency to throw off lateral branches which become highly specialised, and soon die out, because they are unable to adapt themselves to new conditions."

7. Comparison of Zeuglodont and Prosqualodont Brains.

The above paper was practically ready for the press when Prof. Elliot Smith received from Tasmania, through the great courtesy of Prof. Flynn of the Zoological Department in the University at Hobart, a splendid cast of the cranial cavity of *Prosqualodon davidi* which he has recently described. Plaster replicas of the skull from which this cast was made were presented by him to the British Museum of Natural History and to the Zoological Department of University College, London. I have had the privilege of studying these casts and the endocranial cast.

The lateral view of this cast (text-fig. 18) reveals an astounding likeness to the Zeuglodont endocranial cast. We meet with the same cerebellar enlargement, expanding forwards over the cerebrum, and quite an enlarged trigeminus.

It is obvious that such striking similarities would not exist in the absence of some close relationship between these forms, but the data will reveal that this relationship is not a filial one as it has frequently been conceived.

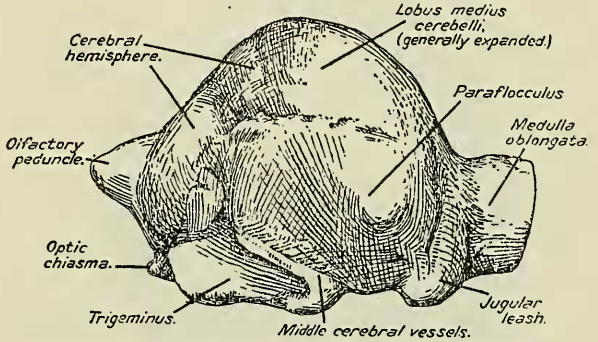
It is to be noted that the paraflocculus is recognizable laterally, but is submerged by a widely and generally expanded cerebellum. The cerebrum is emancipating itself from the cerebellar growth as its great height posteriorly shows. Anteriorly the rapidly dwindling olfactory apparatus is attached in a "nipple-like" fashion to the cerebrum and considerably ventral to it is a well-marked optic chiasma. The middle cerebral vessels reveal a course comparable with that seen in the Zeuglodonts and posteriorly there is a well-marked jugular leash.

The dorsal view corroborates what we have already detected from the lateral aspect. The wide expanse of the "area crescens" cerebelli is the most obtrusive feature and after that the expanding cerebrum. The double olfactory peduncle is clearly seen but no Gasserian ganglion is visible (text-fig. 19).

The posterior view is instructive in revealing an enlarged oval transverse section of the medulla oblongata and still further illustrates the nature of the cerebellar expansion (text-fig. 20).

Perhaps the most informative of all is the ventral view, because we are able to recognise the true size of the trigeminus (which is quite large), the relatively enormous width of the base of the brain, the marked development of the optic chiasma, and the relative atrophy of the olfactory apparatus. There is an entire absence in this brain of anything corresponding to the tuberculum olfactorium or "intertubercular sulcus" of the Zeuglodonts, but we find a ridge on either side of the middle line medial

Text-figure 18.



Lateral view of endocranial cast of *Prosqualodon davidi* Flynn. About ⅓ nat. size.

to the trigeminal region which may be due to the carotid artery and accompanying venous sinuses. The tuber cinereum is not apparent in the cast, but must lie between these ridges (text-fig. 21).

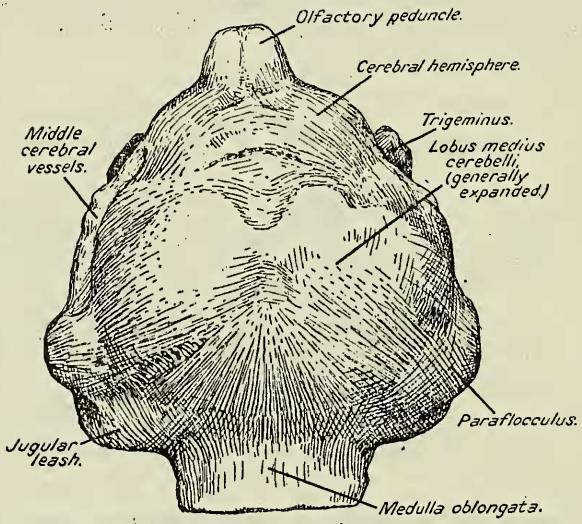
Prosqualodon davidi Flynn comes from the Miocene deposits of Tasmania, and the characters which it presents linking it to the Zeuglodonts might well be interpreted as illustrating its origin from the Zeuglodont family if our information were not so complete as it is now.

The actual bulk of this endocranial cast is approximately 750 c.c., *i.e.*, not quite so great as that of *Zeuglodon intermedius*. This fact itself is sufficient to show that the Eocene form which gave rise to *Prosqualodon* must have possessed a brain-capacity very much less than that of *Prozeuglodon atrox* or of *Zeuglodon intermedius*. This follows from the well-known "law of increasing brain weight" put forward by Marsh and supported by all

palæontological endocranial investigation up to the present time.

Quite apart from this there is ample evidence against the view that a Zeuglodont, even one so primitive as *Prozeuglodon*, could have given rise to *Prosqualodon*. This is very evident if we call to mind those features pointed out in detail for *Zeuglodon sensitivus* (*vide* text-fig. 3) and repeated by all the Zeuglodonts. It was shown in that case that the site of the insertion of the olfactory peduncle in the Zeuglodonts had been drawn, as it were, during atrophy under the fore brain on to the basal aspect. This contraction of the area between the olfactory peduncles and the tuber cinereum demonstrated for us the relative atrophy of the

Text-figure 19.



Dorsal view of endocranial cast of *Prosqualodon davidi* Flynn. About ⅓ nat. size.

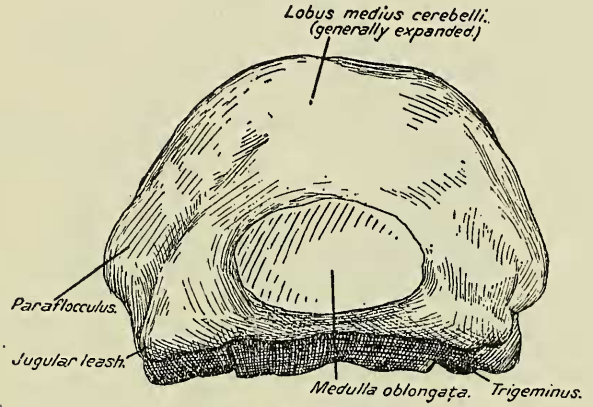
optic chiasmatic region in Zeuglodonts, and, fortunately, the cast of *Prozeuglodon atrox* in this crucial region is sufficiently perfect to illustrate the fact that these changes were already well marked in the Zeuglodonts of the earliest Middle Eocene deposits of the Fayum (*vide* text-fig. 11).

In the case of *Prosqualodon davidi*, on the other hand, we find that the course of its evolution has been entirely different. There is evidence here of an initial expanding of this basal area between the insertion of the olfactory peduncle (*vide* text-fig. 21) and the tuber cinereum (which lies somewhere between the "carotid ridges"). Crossing this wide interspace in *Prosqualodon davidi* we find in the well-defined optic chiasma the evidence of

the retention of elaborate visual capacities in the Miocene—an utter impossibility in the offspring of the Zeuglodonts here described at any epoch.

It is of some value to appreciate how great a degree of trigeminal specialisation is compatible with future evolution. For it is evident that *Prosqualodon davidi* has an enlarged trigeminus, even though we do not find such gross enlargement of the Gasserian ganglia as in the Zeuglodonts. It has already been indicated that "a certain degree of trigeminal specialisation" is to be expected in the ancestors of Cetacea. It seems unquestionable that the initial widening of the Prosqualodont, as well as that of the Zeuglodont, brain and medulla oblongata is due not merely to the passive recession of the sense of smell but rather to the active hypertrophy of the trigeminal apparatus, which in an aquatic mammal provides so much more information

Text-figure 20.



Posterior view of endocranial cast of *Prosqualodon davidi* Flynn. About ⅔ nat. size.

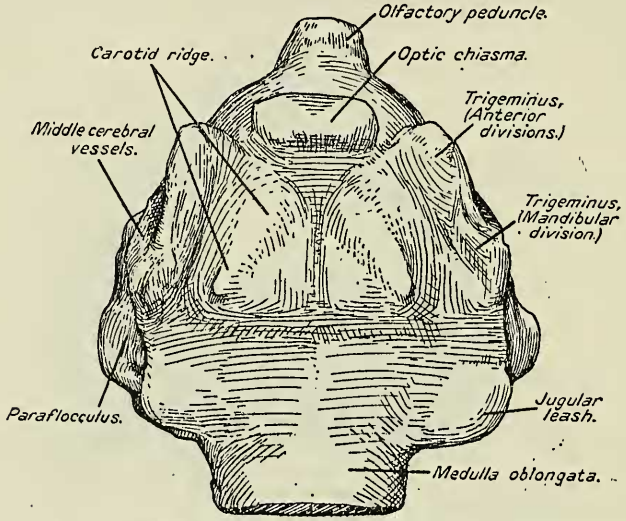
concerning food, friends, and foes than do the senses of smell or sight.

Prosqualodon davidi teaches us therefore that the evolution of the Cetacean stock, while it depended to some degree upon an initial trigeminal specialisation, was not effected by any sudden reliance upon this sense to the neglect of other important senses, but depended upon an orderly and "balanced" correlation of this hypertrophy with a concurrent aggrandisement of the visual and auditory senses. In this connection it is significant that the most expanded portions of the fore brain in *Prosqualodon davidi* appear to be the "occipital" and "temporal" regions; *i. e.*, posteriorly and laterally, where one may reasonably conclude that these senses were finding cerebral representation. Whether Fraas is correct in believing that even the more primitive *Protocetus*

is also off the main line of Cetacean evolution would probably be indicated by an examination of the endocranial casts with regard to these details.

The conformation of the district between the olfactory peduncles and the chiasma—in fact, the whole "mamma-like" appearance of the antero-ventral portion of the fore brain in *Prosqualodon davidi*, contrasting as it does with the same region in the Zeuglodonts—is consonant with the homologous region in true Cetacea. A comparison of this region with the ventral aspect of the brain in the fœtal *Monodon* or adult *Kogia* (*vide* figures in Elliot Smith's account, 1903) demonstrates the truth of the conception that the ancestors of true Cetacea went through

Text-figure 21.



Ventral view of endocranial cast of *Prosqualodon davidi* Flynn. About ⅓ nat. size.

a stage of "expansion of the basal regions of the brain" (witness the "desert region" of Broca in Cetacea) not displayed by Zeuglodonts but evident enough in *Prosqualodon*.

What this expanded "desert region" or tuberculum olfactorium in whales exactly signifies, we are not as yet able to definitely state. Since this area is the site of the palæostriatal cortex overlying the palæostriatum (Dart, 1920) it follows that the persistence of a large "desert region" is dependent on factors other than olfactory, *i. e.*, factors which have determined the size of the palæostriatum itself. The consideration of what these factors actually may be lies outside the scope of this article, but the essential point affecting our argument here is that these

factors, whatever their nature, played an enhanced rôle in the ancestors of Cetacea, whereas they were recessive and negligible in the Zeuglodontidæ.

The evidence afforded by this cast therefore supports the conclusions which we drew in the earlier part of this paper concerning the deflection of the Zeuglodont line from the course of true Cetacean evolution, but supports the conception that *Squalodon* has at least close affinities with the true Cetacean stock.

8. The Trigeminus and the Law of Infiltration in Cerebellar Evolution.

In conclusion, it is necessary to call to mind certain general facts about the cerebellum which appear to throw light upon the strange and generalised hypertrophy of that organ in this group.

We know that animals with very sensitive whiskers and bristles (such as certain Rodentia) depend largely for their power of equilibration upon stimuli which arise in nerve-endings situated in relation with the proximal end of these whisker-like structures and affected by their faintest movement. Such stimuli are communicated to the cerebellum by way of the trigeminus. In *Ornithorhynchus*, instead of bristles, there is a remarkable development of special receptive end organs in the delicate snout served by the trigeminus. The bristles round the mouth-parts of the Sirenia may be active in a similar way in addition to their function as tactile end organs.

The more recent researches of Ingvar (1918) have placed the morphological survey of the cerebellum by Elliot Smith upon an even firmer basis: for he has extended his research into the Reptilian and Avian series and has shown that here, too, the same sulci and three lobes are distinguishable. Such a division into three lobes does not appear to obtain in Fishes or Amphibia. It seems therefore that the advent of the middle lobe synchronises with the origin of a neopallium in the cerebral cortex. The researches of Haller (1900), of Unger (1906), and of Crosby (1917) have shown that the first clearly defined neopallium primordium makes its appearance in the Reptilia, and in these creatures the tripartite structure of the cerebellum is also clearly to be recognised for the first time.

Recognising the relationship which the development of the neopallium has to the expansion of the cerebellum in Mammalia it is, at first, most disconcerting to find in a group of Eocene mammals with such ill-developed neopallium a cerebellum of extravagant proportions which has not merely obliterated all traces of the mid-brain from the surface but threatens to cover the cerebrum also by its forward expansion.

The cerebellum is usually relatively large in Eocene mammals and yet such a bizarre arrangement as is present in Zeuglodonts can have only one explanation. We may eliminate the neopallium

as an explanation because of its slight development and the doubtful presence of a pons Varolii, and it is equally unlikely that the spino-cerebellar contribution could have been so great as to account for the whole of the cerebellar expansion. But we do know that so diminutive and primitive a mammal as *Ornithorhynchus*, with a well-developed trigeminal apparatus can and does possess not only an unexpectedly large neopallium, but also a relatively large convoluted cerebellum. The absolute and the relative size of the Gasserian ganglia in *Zeuglodon sensitivus*, and indeed in all Zeuglodontidæ here represented, are far more striking than they are in *Ornithorhynchus*. There can be no doubt that the afferent impulses reaching the cerebellum from the anterior end of the body in Zeuglodontidæ were of particular value in supplying these animals with information concerning disturbances of equilibration. The distribution of the trigeminal tract within the cerebellum is not fully known, but it is believed by many investigators that in Mammalia there is a tract for conveying trigeminal impulses to the cerebellum. The huge cerebellum in the Zeuglodontidæ may well be due to the fact that, by a rapid and hypertrophic development, the trigeminus provided it with very precise information concerning its position in space and hence afforded to this primitive creature a ready solution of the problem of equilibration in a fluid medium.

I have said that the distribution of a direct trigeminal tract within the cerebellum is not fully known; it would be nearer the truth to state that it is frequently affirmed but is sometimes denied. Since such denial exists it is valuable to put forward other supporting evidence. It seems to me that the denial of the existence of a direct trigeminal connection with the cerebellum can only come from an imperfect appreciation of the developmental history of the cerebellum and a consequent failure to recognise its extent in the brain-axis—or else from a tendency, very manifest during the last two decades, to regard the cerebellum as an overgrown part of the vestibular apparatus.

As regards the development of the cerebellum it must be remembered that the cerebellar ridge first appears in early embryos much further forward in the hind brain (metencephalon) than would be anticipated on the "vestibular" hypothesis. Even in human developmental history, the nerve which is more obviously associated with the cerebellum is the trigeminal and not the vestibular. Ingvar (1918) finds that "Die Basis (cerebelli) ist frontalwärts gerichtet. Von dem ventralen Rande dieser Basis laufen die kräftig entwickelten N. N. Trigemini aus"; or (on p. 343) "Ventralwärts grenzen die Cerebellarwülste an die Insertionstelle des Trigeminus."

It is not absolutely certain what actual neuromere of the hind brain gives rise to the cerebellum, nor is that question pertinent to the present discussion. The embryological facts significant here are: (1) that the cerebellum arises in the most anterior portion of the hind-brain roof, and (2) that the territory of the

neural tube in this vicinity is associated in the vertebrate embryo with the trigeminus (*cf.* Wilson and Hill, 1902; Streeter, 1908), while the acoustico-facialis mass lies entirely posterior to the trigeminus and is related to a different territory which lies medial to it. Hence, any encroachment of vestibular fibres from its territory of the neural tube into the territory which is related to the trigeminus is a secondary phenomenon whether considered phylogenetically or ontogenetically, even though such fibres be direct fibres. In other words, the appearance of vestibular fibres in the cerebellar region is an intrusion just as certainly as is the appearance of the mesencephalic fibres of the trigeminal in the mid-brain, or of thalamic fibres in the fore brain.

The simplest cerebella reproduce more or less faithfully this condition characteristic of the embryos of all Vertebrates. They are mere ridges roofing the most anterior portion of the fourth ventricle and are consequently a link between trigeminal territories and contain decussations of the trochlear and trigeminal nerves (Herrick, 1914; Larsell, 1920; Palmgren, 1921).

In the simplest cerebella *intrusions* of alien fibres are already found, even as we find alien fibres in the simplest-known fore brain and tectum opticum. These *intrusions* occur in the cerebellum in such a way that just as we find the olfactory apparatus is relegated to the periphery of the fore brain and the optic fibres to the periphery of the mid-brain, so we find that the trigeminal territory forms the true fringe of the cerebellum. Consequently, Beccari, Ingvar, and others (Kappers, 1921) have found a direct distribution of the trigeminus to the cerebellum (*e. g.*, in Reptilia).

Topographically, the contribution of the vestibular nerve to the cerebellum is always surrounded by the trigeminal territory and the fibres proceeding to the cerebellum therefrom. Ingvar (1918) has shown (in Mammalia) a distribution of the vestibular component mainly in the flocculus, lingula, and nodulus, and thus *peripherally* to the still more recent intrusions of spino-cerebellar contributions. On the other hand, spino- and olivo-cerebellar fibres have not been demonstrated in such peripherally lying parts such as the lobus flocculoris, and it is to be noted (*vide* Kappers, 1921) that this region is not dependent upon a cerebro-pontine contribution; whereas the clinical researches of Winkler have corroborated the conception that the latest portions of the cerebellum in the phylogenetic sense are more centrally situated.

This "laminar" arrangement of the cerebellar constitution, as it might be termed, although not so clearly defined as the somewhat similar arrangement of successive fibre-intrusions into the fore brain, is nevertheless present. It is to be expected also from the fact that those tracts, which later in phylogeny become incorporated with any region, attain this incorporation by *infiltration* and a spreading apart of the pre-existing mechanism.

The arrangement may be expressed by stating that the vestibular, olivary, spinal, and cerebro-pontine contributions successively come to reach the cerebellum by penetrating a territory which was originally, and so ancestrally, trigeminal.

As has been suggested already, this phenomenon of "penetration" may be illustrated equally well by the *infiltrations* of the mid-brain, thalamus, or fore brain, or by the *infiltration* of the hippocampal commissure by the corpus callosum in the fore brain of Mammalia as shown by Elliot Smith. In brief, if we accept the doctrine of the segmental arrangement of the neural tube elements, it is to be anticipated that the principle finds illustration in the development of the majority of the inter-segmental and supra-segmental apparatuses.

The language of neurology is devoid of any term which describes conveniently this uniformity of behaviour in the laying-down of subsequent formations in the neural tube. It should prove of service therefore to descriptive neurology to recognise in this uniformity the consistent working of a general principle which underlies the whole architecture of the brain and which we may term for convenience the *Law of Infiltration.*

By an inverse reasoning, if this law is correctly conceived, a *peripheral* or *fringing* arrangement of the trigeminal territory itself, and of fibres known to proceed to the cerebellum from it, corroborates the identification of the trigeminal apparatus with the cerebellum and the function of equilibrium, more primitively even than the vestibular apparatus.

These matters have been neglected by those who assert that the auricle of the cerebellum, or lobus flocccularis (Kappers, 1921), is the *oldest* part of the cerebellum. It is not the auricle, but the anterior medullary velum which would better deserve this appellation. The "vestibular" hypothesis has been attractive because it has seemed to demonstrate the fact that the cerebellum was "equilibratory" from the beginning. But this hypothesis tends to ignore the equilibratory potential of all tactile sense, it fails to account for the existence of a cerebellum (Cyclostomes) which has no auricle, and does not account in any way for the striking relationship which the trigeminal nerve always has to the cerebellum in all Vertebrata.

The fifth nerve displays a relationship to that segment of the neural tube, in which the cerebellum becomes developed, which is paralleled only by the relationship of the olfactory nerve to that segment of the tube in which the prosencephalon, and of the optic nerve to that segment in which the mesencephalon is developed. The oldest part of the organ is the trigeminal territory itself just as the olfactory sensorium was the oldest representative of a fore brain and the visual sensorium of a mid-brain.

I have discovered that Spitzka (1886) put forward a somewhat similar view concerning the cerebellum nearly forty years ago :—
"I am inclined to consider it as a homologue of the gelatinous nucleus of the fifth pair, and as in a primitive relation with that

nerve; that subsequently the auditory nerve entered into connection with it, and that, increasing in dimension with its increasing neural connections, it attained the high development found in the human cerebellum through the spinal and cerebral tracts that are detached into its medullary substance." Therefore the present statement of this relationship, although more detailed, cannot be regarded as a novelty.

If we consider the nature of the influences at work in the production of the early chordate brain, it is evident that the more anterior segments were concerned in the production of the olfactory and visual specialisations. These specialisations were bought at the price of successive anterior segments of the primitive vertebrate skin and neural tube. When these anterior segments lost by their specialisation the capacity for the appreciation of *pressure*, the succeeding segment which retained this power grew forward invading the territory of the more specialised segments lying anterior to it. Such an invasion meant an increase or hypertrophy of this (trigeminal) segment and a specialisation within it of the *tactile* function. How exuberant has been its response to this demand is demonstrated by the fact that—amongst Mammalia, for instance—it subserves the tactile sense for the entire region anterior to the second cervical nerve, with the exception of the vestigial somatic elements of the vagus (Arnold's nerve).

The information conveyed by the trigeminal system proved extremely valuable, because it told the animal so much about what moved in space around it and also *about its own position in space*. Hence the central processes from the trigeminal ganglion assumed a sudden reflex ascendency over an increasing number of the succeeding segmental nerves through the radix descendens and the substantia gelatinosa Rolandi in most Vertebrata. Even in Man the descending root of the trigeminal represents one of the most impressive features of the medulla oblongata. Always a striking feature in Mammalia, this reflex dominance is shown to its best advantage (in living forms) in *Ornithorhynchus*; in this creature the trigeminal seems to exert a reflex control over practically the whole of the spinal cord.

Thus there has been a downward encroachment of the trigeminus upon lower segments of the medulla oblongata in a fashion comparable with the upward encroachment of the vestibular nerve into the trigeminal territory or of the mesencephalic root of the trigeminal upon optic territory. It is a further example of the *Law of Infiltration*. Seemingly this encroachment afforded the bridge whereby the spino-cerebellar systems were conducted to the originally trigeminal territory of the cerebellum. For the spinal fibres naturally lay *peripheral* to the infiltrating descending root of the trigeminus, and as the spinal fibres coursed towards the cerebellum they came to embrace the trigeminus trunk before piercing its territory to enter the cerebellum. The differentiation into anterior and posterior spino-cerebellar tracts emerged from

a relationship primarily not to the cerebellum as such, but to the trigeminus.

So, in addition to the *fringing* above mentioned, a graphic picture of the central role which the trigeminal has played in the origin of the cerebellum is afforded by the relation of the anterior and posterior spino-cerebellar tracts to the trigeminal nerve (in most Vertebrata) and by the central position of the trigeminus in the pons (in higher Mammalia).

Considering the nature of the impulses it conveyed, it is not surprising that the trigeminal nerve, which has had such diverse evolutionary possibilities in all vertebrate groups, should have been very intimately concerned in the emergence and evolution of the cerebellum in Vertebrata. Nor is it surprising that we should find illustrated in the Zeuglodontidæ a group of primitive mammals taking to a water life at a stage so plastic that the trigeminal apparatus should become sufficiently specialised and hypertrophic to determine, through its moulding of the cerebellum and the spinal cord, the whole course of evolution (or devolution) of its central nervous system.

9. Note on the Skulls from which the Endocranial Casts described by Dr. Dart were taken. By C. W. Andrews, D.Sc., F.R.S. (British Museum of Natural History.)

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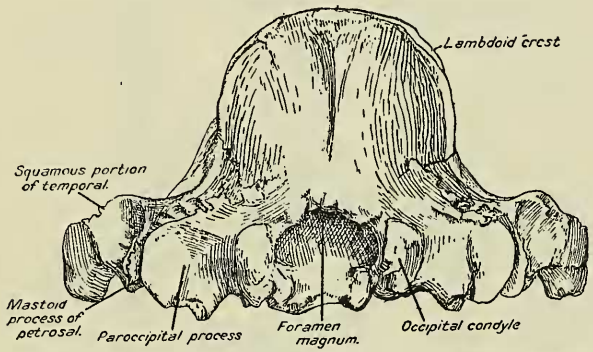
Unfortunately, from the nature of the case, the skulls belonging to the two natural casts above described are unknown, having been destroyed by weathering, but those from which the remaining casts were made are preserved and are here discussed. Four such skulls are known. Of these, two [M. 8150 (a cast) and M. 10228] certainly belong to *Zeuglodon osiris* Dames, from the Qasr-el-Sagha beds (Upper Mokattam = Bartonian), north of Lake Birket-el-Qurun in the Fayum. One (M. 9266) is the skull of *Prozeuglodon atrox* Andrews, from the lower part of the Birket-el-Qurun beds in a valley twelve kilometres W.S.W. of the Gar-el-Gehannem, lying to the west of the lake. This last specimen may be regarded as the paratype of the species and is described and figured in the British Museum Catalogue of the Fossil Vertebrata of the Fayum (1906, p. 243). The fourth skull (M. 10173), forming the middle term of the series, seems from the nature of the matrix to have been obtained from the Birket-el-Qurun beds at the western end of the lake, from an horizon intermediate between those from which the other species were found. This, however, in the absence of definite information from the collector is not certain. This skull appears to belong to a hitherto-undescribed species which has been called *Zeuglodon intermedius* by Dr. Dart, the characters of which are given below.

Numerous other Zeuglodont remains have been collected from various horizons in Egypt, and there is some difference of opinion

as to their determination and relationship to one another. For the purposes of the present paper these may be disregarded and the series represented by *Prozeuglodon atrox*, *Zeuglodon intermedius*, and *Zeuglodon osiris* alone considered. The characters of the skulls of these species completely support Dr. Dart's conclusion, founded on the endocranial casts, that these three species represent terms in a phyletic series.

The skull of *Prozeuglodon* has been described in detail in the catalogue (*loc. cit.*), so that here it will only be necessary to refer to a few characters easily comparable with those of the other forms. The occipital surface (text-fig. 22) above the foramen magnum is wider than high (if the height* be taken as 100, the width is 110) and it is only gently concave from side to side. The foramen magnum and the occipital condyles are both large. The convexity of the portion of the cranial wall formed by the parietal

Text-figure 22.



Occipital surface of skull of *Prozeuglodon atrox* Andrews. M. 9266. About ¼ nat. size.

and squamosal is greater than in the later forms, while the sagittal crest is much less developed. The posterior border of the narial opening is over the space between the first and second premolars and the snout is less prolonged anteriorly than in the later forms. Some of the above peculiarities may be dependent to some extent on the circumstance that the skull described is not quite adult.

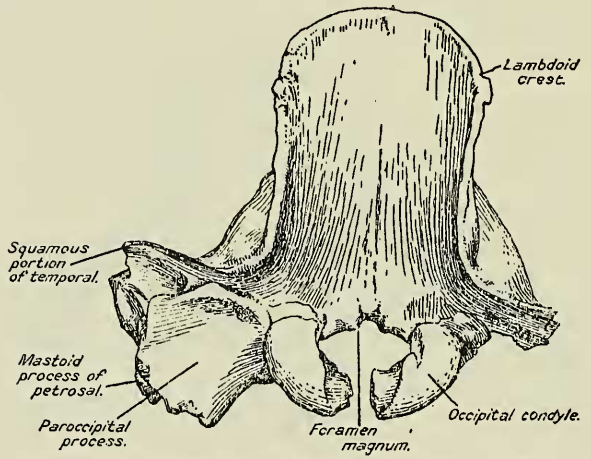
The type-skull M. 10173 of *Zeuglodon internedius* (text-fig. 23) is not complete, the zygomatic arch and the terminal portion of the snout being missing; the teeth also are much broken. In it the width of the occipital surface (text-fig. 23) is much less in proportion to its height* (height 100, width 66), and it is much more concave from side to side than in *Prozeuglodon*.

* In each case the height is measured from the upper border of the foramen magnum to the point of union of the sagittal and lambdoidal crests.

But the concavity is regular and the middle portion of the lambdoidal crest is not suddenly reflected backwards as in *Zeuglodon osiris*. The occipital condyles and foramen magnum are relatively smaller than in *Prozeuglodon*, the occipital crest more developed, and the convexity of the lateral cranial surface less marked. The snout was more slender and more prolonged in front of the narial opening than in *Prozeuglodon*.

This skull, both in the form of its occipital surface and in other points, closely resembles that described by Stromer as *Zeuglodon osiris* (in his paper of 1908) and distinguished by him as Mn.9. It is very different from that described by the same writer as *Zeuglodon osiris* in 1903 and called in his later paper Mn.1. This latter seems to be the true *Zeuglodon osiris*, its lower jaw

Text-figure 23.



Occipital surface of skull of *Zeuglodon intermedius*, sp. n. M. 10173. About $\frac{1}{4}$ nat. size.

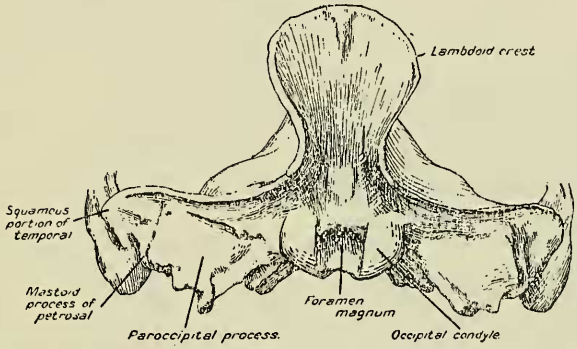
agreeing very closely with that of the type-specimen of the species as described and figured by Dames (1894). Mn.9 is either the present species (*Zeuglodon intermedius*) or a form between it and *Prozeuglodon*.

The skulls of *Zeuglodon osiris* from which endocranial casts have been made are two in number. One (M. 8150) is very incomplete and reveals only the dorsal contour of the brain. The endocranial cast of this skull was figured and described by Prof. Elliot Smith (1903). The other skull (M. 10228) is a nearly perfect specimen, and in order that the endocranial cast might be made it was skilfully cut into sections and the matrix removed by Mr. L. E. Parsons (text-fig. 24).

The occipital region of this skull agrees exactly with Stromer's

specimen Mn.1. It is remarkable for its extreme narrowness compared with its height, the lateral portions of the lambdoidal crests being sharply deflected backwards so that the deeply concave occipital surface has the appearance of being pinched in at the sides. This character is also well shown in the cast of the second skull (M. 8150). If the height be taken as 100 the width is about 44. The occipital condyles and foramen magnum are

Text-figure 24.



Occipital surface of skull of *Zeuglodon osiris* Dames. M. 10228. About $\frac{1}{5}$ nat. size.

still smaller than in *Zeuglodon intermedius* and the convex sagittal crest is much higher. The side walls of the skull show little traces of convexity. The snout seems to have been relatively narrower and perhaps the nostril opened rather further back than in *Zeuglodon intermedius*.

The changes occurring in the stages described are:—

(1) Increasing narrowness and concavity of the occipital surface above the foramen magnum, due mainly to the folding back of the high lambdoidal crests;
(2) increased height of the sagittal crest;
(3) the reduction in the size in the condyles and foramen magnum;
(4) decreasing convexity of the lateral cranial walls accompanying the depression of the upper portion of the brain;
(5) the increase in length and slenderness of the snout and the probable recession, to some extent, of the narial opening.

Changes (1) and (2) result in the increase of the surface for the attachment of the jaw-muscles, and are no doubt correlated with the increasing size and strength of the mandible.

In *Prozeuglodon* the two posterior upper premolars have a large

postero-internal buttress supported by a large distinct root. In the two species of *Zeuglodon* this buttress is reduced in size and probably had no distinct root, though from the state of preservation of the specimen this cannot be definitely settled.

Some dimensions in millimetres of the skull in the three forms are given below. These in some instances must be regarded as approximate only:—

	Prozeuglodon. (M. 9266.)	*Z. intermedius.* (M. 10173.)	*Z. osiris.* (M. 10228.)
Length from condyles to tip of snout	673	550	543 app.
Length from lambda to nasal opening	403 app.	453	467
Height of occipital surface from foramen magnum to lambda	120	160	156
Least width of occipital surface between lambdoidal crests	129	106	69
Width across occipital condyles	108	112	92
Width across postorbital processes	264	283	293
Width of foramen magnum	55	52	46
Length of parietal portion of sagittal crest	125	157 app.	170

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